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PRELIMINARY STUDIES ON THE VEGETATION OF AN OLD-FIELD COMMUNITY IN SOUTHEASTERN MICHIGAN

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INTRODUCTION

THE community has long been recognized as a natural unit of ecological organization, but its complexity is so great that our knowledge of community structure and function is little better than superficial. Yet there is need for a thorough understanding of the dynamics of communities and of the manner in which they are maintained as recognizable entities. The sudden and generally severe alterations in the dynamic balance of nature which are caused by the rapidly expanding influence of man upon his environment call for a renewed effort to investigate and to comprehend the numerous factors and forces which integrate and regulate communities.

A long-term project to study the complete biota and the organization and operation of a natural community was initiated in the summer of 1948 by the Laboratory of Vertebrate Biology of the University of Michigan. Among the ultimate objectives of this study are a description of the community in terms of its energy utilization and of its productivity as a biological system and a comprehension of the mechanisms involved in its maintenance as a natural unit. The development of satisfactory techniques to achieve these objectives will of necessity constitute an important part of the work. It is expected that the ideas and methods which arise from this study will be, at least in part, applicable to other types of communities.

Several criteria were held to be of importance in the selection of a

community for these purposes. Such a community should be as free from present human disturbance as possible, and this freedom should be guaranteed for the duration of the study, however long that might be. The structure of the community should be relatively simple, for, in general, the less complex the community, the more easily can we discern its life processes. The nature of the surrounding environment must be taken into account, since the proximity of other different communities may have a profound effect upon the character of the unit under study. The size of area to be investigated is also important, for it must be small enough to be examined effectively, yet large enough to give representative and reliable results. Accessibility at all times of year would greatly facilitate an investigation of the sort contemplated here.

The most satisfactory combination of these conditions that was readily available was that provided by an abandoned field on the Edwin S. George Reserve, of the University of Michigan, Livingston County, Michigan, near the town of Pinckney and about 25 miles northwest of Ann Arbor. Through the generosity of the late Colonel George, a tract of approximately two square miles was given to the University in 1930 for the establishment of a natural-history reserve. Since 1928 it has been under game fence, free from fire or human interference with successional changes. In climate, physiography, and types of habitat it is representative of much of the surrounding region.

Descriptions of various aspects of the biology and ecology of the George Reserve have already been published (Blair, 1948; Burt, 1940; Cantrall, 1943; Howard, 1950; Rogers, 1942; Sutton, 1949). Cantrall (1943) has provided a general description of the area, together with an aerial photograph and a contour map. Much of this information has proved helpful in the preliminary stages of the investigation of the old-field community under study. The ecologist needs to call upon many specialists for assistance, not only for determination of the species with which he is dealing, but also concerning environmental features such as soil and quantitative techniques such as sampling methods.

The present paper is intended to be an introductory description of the vegetation of the field selected as a site for this study. It is the composition and structure of the vegetation which gives this community its characteristic appearance.

Acknowledgments

We are much indebted to J. Speed Rogers, Director of the Edwin S. George Reserve, for making the facilities of the Reserve available for this study. We should also like to thank Joyce H. Jones, William C. Steere, and Rogers McVaugh for determining and checking the identifications of lichens, mosses, and seed plants, respectively. Maurice W. Senstius very kindly identified the soil type and series for the samples obtained by Nelson G. Hairston and F. C. Evans. Victor J. Brookes, R. DeWitt Ivey, Dixon L. Riggs, and Fernando Segadas-Vianna assisted in taking samples of the vegetation, and Mrs. Emmy Hesz and D. L. Riggs weighed the material collected from the clipped quadrats. Lee R. Dice gave many helpful suggestions in the preparation of this manuscript.

GENERAL DESCRIPTION OF FIELD

The field under study is a 15-acre tract situated in the northeast quarter of section 19 of Putnam Township, lying a few hundred yards north of the Colonel George house, on a large glacial outwash plain in the central and highest part of the Reserve, at an elevation of 975 to 1000 feet. To the east of this plain is an esker-like formation, half-a-mile long, which is bordered by a series of kettle holes and deep depressions. These features are largely the result of the effects of ice and of the glacial waters of the ancestral Huron River drainage at the close of the Wisconsin glaciation. A diagram of the study area and its immediate environs is shown in Figure 1. The field is approximately 220 yards in width and 360 yards in length, and the long axis is oriented almost exactly due north.

History

The field is bordered on much of its periphery by oak-hickory woods. This same forest type evidently covered the field prior to clearing, which is believed to have been done early in the second half of the past century. Cultivation of the cleared fields on the uplands of the Reserve was carried on extensively before 1900 (Cantrall, 1943: 32). After the turn of the century these areas were increasingly given over to use as pastures, doubtless in part because of the generally sterile nature of the soil. For the past two decades, however, during which it has been under game fence as part of the Reserve, the field has not been subject to pasturing or other disturbance, although the maintenance of a sizable deer herd on the Reserve (O'Roke and Hamerstrom, 1948) has unquestionably been a factor in the slow rate at which the return to forest conditions is progressing.

Physiography

The present surface of the field has a gently rolling appearance, marked by a number of shallow depressions or swales which are concentrated largely in the northern half (Fig. 1). Approaching from the south, one encounters a slight rise culminating about mid-field and receding as gradually to the north. The ground slopes away sharply to the west and in the wooded area along the eastern margin. These slopes and swales determine the clearly marked drainage pattern. Several details of the field are shown in Plates I and II.

Climate

The present-day climate of the region in which the Reserve is located is a humid type characterized by low thermal efficiency and by

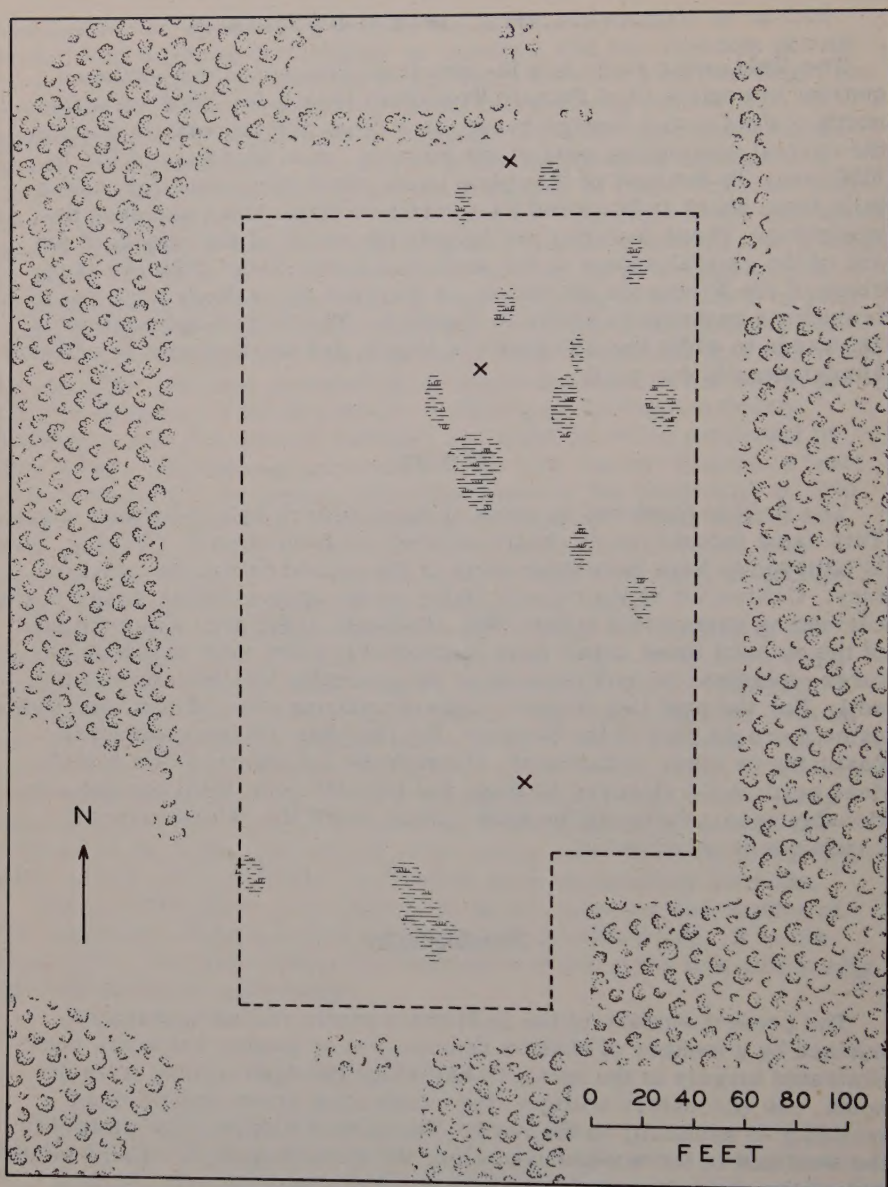


FIG. 1. Diagram of old field and environs, Edwin S. George Reserve, Livingston County, Michigan. X = single large hickories. Grassland represented by blank area. Dashed line indicates boundaries of study area.



Oak-hickory woods



"Swales"

rainfall throughout the year. This area lies on the boundary between the Dfb and the Dfa climatic zones of the Köppen system as revised by Ackerman (1941) for North America. In the Thornthwaite (1931) system, this climate is designated as BC'r. Data presented by Cantrall (1943) indicate the prevailing average annual precipitation to be about 30 inches and the range of mean monthly temperatures to be from approximately 22° F. in January to about 72° F. in June and July; the growing season is stated to be about 145 days. The exposed situation of the field makes it especially vulnerable to such weather extremes as strong winds, but as yet no detailed study of microclimates in the area has been made.

Soil

The soil that has developed under these conditions of physiography and climate is a gray-brown, podzolic, sandy loam belonging to the Fox series. Soil samples taken by N. G. Hairston and F. C. Evans showed that in the higher part of the field the dark-brown, organic horizon seldom exceeds a depth of 9 inches, whereas in the swales this same horizon extends as a thick phase to a depth of 2 or 3 feet. Beneath this dark-brown layer lies the B horizon, with a characteristic orange-red color resulting from the accumulation of ferric iron. The orange sand gradually gives way to a gray gravel which reaches a depth of at least 74 inches, the limits of our samples.

FLORISTIC COMPOSITION

Upon first sight the vegetation of the field appears to be more or less homogeneous and is clearly dominated by grasses. One is soon aware, however, of the existence of two principal community types, associated with the swales or depressions and the more elevated or upland areas of the field, respectively.

The swales, which are noticeably moister than the higher levels, support a dense growth of *Poa pratensis*, which forms a virtually closed community, although such forbs as *Asclepias syriaca* and *Cirsium vulgare* eventually gain footing. A conspicuous border of one or more species of *Setaria* is frequently found, completely or partly enclosing the swale. The vegetation in these depressions remains green long after the upland vegetation has dried up, and the contrast between the two is especially prominent in the late summer, though also conspicuous at other times of year (Pl. I, Fig. 1).

The major part of the vegetation is on the upland areas, which cover approximately 14.5 of the 15 acres occupied by the field. This community type is dominated by *Poa compressa* and the later-flowering *Aristida purpurascens*; interspersed with these are a number of other grasses, most notably several species of *Panicum*, and a considerable variety of associated forbs. Several of the latter, such as *Antennaria neglecta* and *A. fallax*, have more or less strongly developed vegetative reproduction and often occur in patches. Others like *Liatris aspera* are also

definitely clumped even in the absence of obvious vegetative propagation, and still others are of sporadic or of more regular occurrence. The result is a community characterized by a marked patchwork or mosaic distribution of most of its component species.

These two community types are of general occurrence throughout the Reserve and the surrounding region. They evidently correspond to the "bluegrass meadow association" and the "bluegrass field association" as described briefly by Blair (1948). Table I lists the vascular plants and macroscopic cryptogams which have thus far been observed in the particular field under study. A total of 112 species is recorded. Most of these occur in the *Poa-Aristida* community of the upland parts of the field, and it is with this assemblage that the remainder of this paper is primarily concerned.

Species-Area Relationship

In order to determine the size of quadrat most satisfactory for sampling purposes, a plot of 2048 square meters, or approximately one-half acre, lying well within an apparently typical part of the *Poa-Aristida* community, was investigated October 22, 1948, with reference to species-area relationships. In one corner of this plot, a quadrat 0.25 square

TABLE I

A List of the Vascular Plants and Macroscopic Cryptogams Observed in an Old-field Grassland Community, Edwin S. George Reserve, Michigan

Nomenclature and sequence of names of lichens, mosses, and seed plants, according to Fink (1935), Steere (1947), and Fernald (1950), respectively.

LICHENS

<i>Peltigera horizontalis</i> (Huds.) Baumg.	<i>Cladonia cariosa</i> (Ach.) Spreng.
<i>Lecidea</i> species	<i>Cladonia cornuta</i> (L.) Schaer.
<i>Cladonia sylvatica</i> (L.) Hoffm.	<i>Cladonia pyxidata</i> (L.) Hoffm.
<i>Cladonia alpestris</i> (L.) Rabenh.	<i>Cladonia verticillata</i> Hoffm.
<i>Cladonia cristatella</i> var. <i>vestita</i> Tuck.	<i>Cladonia verticillata</i> var. <i>cervicornis</i>
<i>Cladonia furcata</i> var. <i>racemosa</i> (Hoffm.)	(Ach.) Flot.
Floerke	<i>Parmelia sulcata</i> Tayl.

MOSESSES

<i>Ceratodon purpureus</i> (Hedw.) Brid.	<i>Eurhynchium pulchellum</i> (Hedw.) Dixon
<i>Ditrichum pallidum</i> (Hedw.) Hampe	<i>Atrichum angustatum</i> (Brid.) BSG
<i>Pleurozium subulatum</i> (Hedw.) Lindb.	<i>Polytrichum juniperinum</i> Hedw.
<i>Bryum caespitium</i> Hedw.	<i>Polytrichum piliferum</i> Hedw.
<i>Brachythecium</i> species	

TABLE I (Continued)

SEED PLANTS

<i>Juniperus communis</i> var. <i>depressa</i> Pursh	<i>Desmodium paniculatum</i> (L.) DC.
<i>Juniperus virginiana</i> L.	<i>Lespedeza virginica</i> (L.) Britt.
<i>Poa compressa</i> L.	<i>Lespedeza capitata</i> Michx.
<i>Poa pratensis</i> L.	<i>Lespedeza hirta</i> (L.) Hornem.
<i>Danthonia spicata</i> (L.) Beauv.	<i>Vicia villosa</i> Roth.
<i>Sporobolus vaginiflorus</i> (Torr.) Wood	<i>Oxalis stricta</i> L.
<i>Agrostis alba</i> L.	<i>Euphorbia corollata</i> L.
<i>Agrostis scabra</i> Willd.	<i>Hypericum perforatum</i> L.
<i>Phleum pratense</i> L.	<i>Lechea villosa</i> Ell.
<i>Aristida purpurascens</i> Poir.	<i>Lechea stricta</i> Leggett
<i>Panicum capillare</i> L.	<i>Viola sagittata</i> Ait.
<i>Panicum depauperatum</i> Muhl.	<i>Oenothera biennis</i> L., or related species
<i>Panicum meridionale</i> Ashe	<i>Oenothera rhombipetala</i> Nutt.
<i>Panicum lanuginosum</i> Ell.	<i>Apocynum androsaemifolium</i> L.
<i>Panicum sphaerocarpon</i> Ell.	<i>Apocynum cannabinum</i> L.
<i>Panicum oligosanthos</i> var. <i>Scribnerianum</i> (Nash) Fern.	<i>Asclepias syriaca</i> L.
<i>Setaria glauca</i> (L.) Beauv.	<i>Lithospermum croceum</i> Fern.
<i>Setaria viridis</i> (L.) Beauv.	<i>Monarda fistulosa</i> L.
<i>Cenchrus longispinus</i> (Hack.) Fern.	<i>Blephilia hirsuta</i> (Pursh) Benth.
<i>Andropogon scoparius</i> Michx.	<i>Hedeoma pulegioides</i> (L.) Pers.
<i>Cyperus filiculmis</i> var. <i>macilentus</i> Fern.	<i>Solanum</i> species
<i>Carex Muhlenbergii</i> var. <i>enervis</i> Boott	<i>Physalis heterophylla</i> Nees
<i>Carex Bicknellii</i> Britt.	<i>Verbascum Thapsus</i> L.
<i>Carex pensylvanica</i> Lam.	<i>Plantago aristata</i> Michx.
<i>Carex</i> species	<i>Galium pilosum</i> Ait.
<i>Juncus tenuis</i> Willd.	<i>Houstonia longifolia</i> Gaertn.
<i>Carya ovalis</i> (Wang.) Sarg.	<i>Vernonia</i> species
<i>Quercus rubra</i> L.	<i>Liatris aspera</i> Michx.
<i>Quercus velutina</i> Lam.	<i>Solidago juncea</i> Ait.
<i>Rumex Acetosella</i> L.	<i>Solidago nemoralis</i> Ait.
<i>Polygonum tenue</i> Michx.	<i>Solidago rigida</i> L.
<i>Anemone cylindrica</i> Gray	<i>Solidago graminifolia</i> (L.) Salisb.
<i>Arabis hirsuta</i> var. <i>pycnocarpa</i> (Hopkins) Rollins	<i>Aster</i> species
<i>Crataegus crus-galli</i> L.	<i>Erigeron strigosus</i> Muhl.
<i>Crataegus</i> species	<i>Erigeron canadensis</i> L.
<i>Fragaria virginiana</i> Duchesne	<i>Antennaria neglecta</i> Greene
<i>Potentilla arguta</i> Pursh	<i>Antennaria fallax</i> Greene
<i>Potentilla argentea</i> L.	<i>Gnaphalium obtusifolium</i> L.
<i>Potentilla recta</i> L.	<i>Ambrosia artemisiifolia</i> L.
<i>Potentilla simplex</i> Michx. (?)	<i>Rudbeckia hirta</i> L.
<i>Rubus flagellaris</i> Willd.	<i>Achillea Millefolium</i> L.
<i>Prunus serotina</i> Ehrh.	<i>Cirsium vulgare</i> (Savi) Tenore
<i>Medicago sativa</i> L.	<i>Krigia virginica</i> (L.) Willd.
<i>Desmodium illinoense</i> Gray	<i>Tragopogon pratensis</i> L.
	<i>Lactuca canadensis</i> L.
	<i>Lactuca pulchella</i> (Pursh) DC.
	<i>Hieracium Gronovii</i> L.
	<i>Hieracium longipilum</i> Torr.

decimeters in area was laid out and the species of plants present recorded. A quadrat double this size and including the first quadrat was next laid out and the species of plants present again listed. This procedure was repeated a number of times to provide a series of quadrats, each with an area twice that of the preceding one and containing all of the smaller quadrats. A transition from the quadrat of 64 square decimeters to one of 100 square decimeters facilitated the laying out of the larger quadrats. The complete series of 21 "nested" quadrats ranged in size from 0.25 to 204,800 square decimeters. Table II lists the species of plants which were observed in this series. The smallest quadrat contained but one species, *Aristida purpurascens*, while a total of 48 species was recorded for the largest quadrat.

Additional species-area data were obtained in June, 1949, when sets of nested quadrats ranging in size from one square decimeter to one square meter were used for sampling the *Poa-Aristida* community. A series of 20 such sets was taken in a systematic or regularized manner, the sets being spaced about 20 meters apart on a grid pattern. Another series was similar in all respects except that the locations of the sets were drawn at random. The number of species per quadrat for each set of these two series is shown in Table III. When each series is considered as a whole and the total number of species found in all quadrats of a given size is recorded, the results for the two series are comparable for all quadrat sizes except the two largest, which contained more species in the randomized series. The species-area curve (Cain, 1938) obtained by plotting number of species per quadrat against quadrat area is shown in Figure 2. The point on the curve which represents an increase of 10 per cent

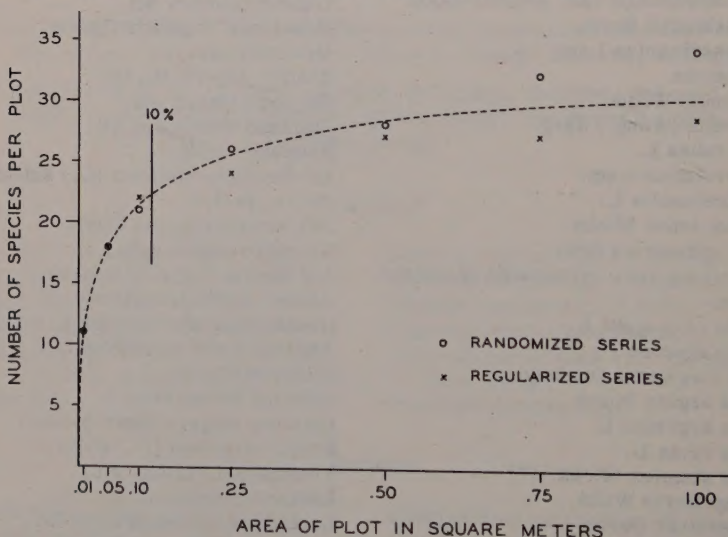


FIG. 2. Species-area relationships obtained from randomized and regularized series of nested plots, *Poa-Aristida* community, Edwin S. George Reserve, Livingston County, Michigan, June 7, 1949. Dashed line represents free-hand curve showing general trend of relationships. Vertical line indicates point on curve at which a 10 per cent increase in sample area gives an increase of 10 per cent in the total number of species sampled.

TABLE II

Occurrence of Plant Species in a Series of Nested Quadrats in a Poa-Aristida Community, Edwin S. George Reserve, October 22, 1948.

One quadrat only of each size examined. x, present; -, absent.

Species	Area in Square Decimeters																					
	0.25	0.50	1	2	4	8	16	32	64	100	200	400	800	1,600	3,200	6,400	12,800	25,600	51,200	102,400	204,800	
<i>Aristida purpurascens</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Rumex Acetosella</i>	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Cladonia verticillata</i>	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Cladonia cristatella</i>	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Poa pratensis</i>	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Poa compressa</i>	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Peltigera horizontalis</i>	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Cladonia cornuta</i>	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Oxalis stricta</i>	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Cladonia pyxidata</i>	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Antennaria fallax</i>	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Panicum meridionale</i>	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Gnaphalium obtusifolium</i>	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Ambrosia artemisiifolia</i>	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	
<i>Aster</i> sp. (sterile rosette)	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	x	
<i>Solidago rigida</i>	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	x	
<i>Liatris aspera</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	
<i>Antennaria neglecta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	x	
<i>Polygonum tenue</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	x	
<i>Solidago nemoralis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x	
<i>Polytrichum piliferum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	
<i>Hieracium longipilum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	
<i>Hieracium Gronovii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	
<i>Panicum oligosanthes</i> var. <i>Scribnerianum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	
<i>Hedeoma pulegioides</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	
<i>Lespedeza capitata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	
<i>Ditrichum pallidum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Tragopogon pratensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Cyperus filiculmis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Monarda fistulosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Panicum depauperatum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Cladonia cariosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Lactuca</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Polytrichum juniperinum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Panicum</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Oenothera biennis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Crataegus crus-galli</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Prunus serotina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Lechea villosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Lecidea</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Asclepias syriaca</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Lespedeza virginica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Setaria glauca</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Potentilla argentea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Juniperus communis</i> var. <i>depressa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Physalis heterophylla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Crataegus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
<i>Cladonia alpestris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	
Total species	1	2	2	3	3	5	7	8	9	13	14	15	19	25	28	33	36	36	41	42	48	

TABLE III

Species-Area Data from Twenty Randomized and Twenty Regularized Sets of Nested Quadrats Used in Sampling the Poa-Aristida Community,
Edwin S. George Reserve, June 7, 1949

Number of Species Per Quadrat															
Randomized Series								Regularized Series							
Plot Size (sq. m.)	0.01	0.05	0.10	0.25	0.50	0.75	1.00	Plot Size (sq. m.)	0.01	0.05	0.10	0.25	0.50	0.75	1.00
Plot Number								Plot Number							
1 ...	3	3	3	4	5	5	6	1 ...	2	4	4	5	6	7	7
2 ...	3	6	7	8	8	10	12	2 ...	2	3	5	7	10	11	12
3 ...	3	4	5	8	8	9	10	3 ...	3	9	11	12	12	14	15
4 ...	1	4	5	7	7	8	9	4 ...	3	5	6	9	10	10	13
5 ...	3	8	8	9	9	11	12	5 ...	4	5	6	7	7	8	9
6 ...	1	4	4	5	6	6	8	6 ...	2	6	7	9	10	11	13
7 ...	4	7	8	9	9	11	11	7 ...	4	4	4	5	7	8	9
8 ...	3	5	5	6	9	9	10	8 ...	2	4	4	6	6	9	9
9 ...	2	5	6	7	8	10	10	9 ...	1	4	7	10	13	15	15
10 ...	4	6	7	8	11	11	11	10 ...	3	6	7	8	9	11	11
11 ...	4	6	6	8	10	12	12	11 ...	3	4	5	6	8	8	10
12 ...	2	5	5	7	8	8	10	12 ...	1	4	4	7	8	8	8
13 ...	3	5	7	10	11	11	13	13 ...	3	3	5	5	6	6	6
14 ...	3	4	5	5	7	8	10	14 ...	3	5	6	7	8	9	9
15 ...	3	4	6	7	8	9	9	15 ...	2	5	6	8	9	9	10
16 ...	3	7	9	11	13	14	14	16 ...	3	3	4	5	7	8	8
17 ...	3	4	6	8	10	10	12	17 ...	3	4	4	5	5	5	7
18 ...	2	5	5	5	6	7	8	18 ...	3	4	4	4	6	6	6
19 ...	3	4	7	12	12	14	15	19 ...	3	4	5	7	9	10	10
20 ...	3	6	7	9	11	11	11	20 ...	2	4	5	6	7	7	7
Total species	11	18	21	26	28	32	34	Total species	11	18	22	24	27	27	28

of the total number of species sampled for an increase of 10 per cent of the total sample area is indicated by a vertical line crossing the curve. Whether one adopts this arbitrary measure proposed by Cain (1938) or relies on the point beyond which the curve flattens and tends to become asymptotic with the abscissa axis, a quadrat size of 0.25 square meters seems to be adequate for sampling this Poa-Aristida community as a whole, provided a sufficient number of samples is taken.

Frequency

Two additional randomized series of 0.25-square-meter quadrats were also collected in June, 1949. The percentage frequencies with which the various species occurred in the one regularized and the three randomized series are shown in Table IV. The results of these series are in general

TABLE IV

Comparison of Frequencies (in Per Cent) of Species from Different Sets of Sample Quadrats (0.25 sq. m. each) in the Grass-dominated Community of an Old Field on the Edwin S. George Reserve, June 6-7, 1949

	Regularized	Randomized Series 1	Randomized Series 2	Randomized Series 3
Number of plots	20	20	20	20
<i>Poa compressa</i>	95	100	100	100
<i>Aristida purpurascens</i>	90	90	80	75
<i>Rumex Acetosella</i>	100	95	100	90
<i>Hedeoma pulegioides</i>	55	80	75	65
<i>Solidago nemoralis</i>	75	70	65	70
<i>Gnaphalium obtusifolium</i> . .	50	40	30	50
<i>Erigeron canadensis</i>	25	35	35	50
<i>Solidago rigida</i>	20	30	30	15
<i>Lespedeza capitata</i>	10	5	10	5
<i>Antennaria neglecta</i>	25	25	20	15
<i>Ambrosia artemisiifolia</i> . .	5	10	15	20
<i>Oxalis stricta</i>	20	25	30	20
<i>Potentilla arguta</i>	...	...	...	5
<i>Hieracium longipilum</i>	20	15	25	20
<i>Panicum oligosanthos</i> var. <i>Scribnerianum</i>	...	15	30	20
<i>Poa pratensis</i>	5	30	20	20
<i>Tragopogon pratensis</i>	...	5	...	15
<i>Asclepias syriaca</i>	5	...	15	5
<i>Oenothera rhombipetala</i> . .	...	...	5	5
<i>Liatris aspera</i>	10	10	15	10
<i>Panicum meridionale</i>	5	10	20	5
<i>Lespedeza virginica</i>	10	...	5	10
<i>Lechea villosa</i>	...	...	...	5
<i>Carex pensylvanica</i>	...	10	...	5
<i>Potentilla argentea</i>	...	...	...	5
<i>Panicum</i> sp.	35	30	30	10
<i>Cyperus filiculmis</i>	...	...	...	10
<i>Antennaria fallax</i>	10	10	5	5
<i>Krigia virginica</i>	5	5	...	10
<i>Solanum</i> sp.	...	...	5	...
<i>Carex</i> sp.	...	5	5	...
<i>Anemone cylindrica</i>	...	5	...	...
<i>Desmodium illinoense</i> . . .	...	5	...	...
<i>Prunus serotina</i> (seedling). .	...	5	...	...
<i>Fragaria virginica</i>	5	...	...	...
<i>Blephilia hirsuta</i>	5	...	...	...
<i>Lactuca</i> sp.	5	...	...	...
No. spp. (Total 37)	24	26	24	29
Average percentage frequency	28.7	29.4	32.1	25.5

closely comparable. In nearly all cases the frequency percentages for the several species are of the same order of magnitude in the different sets of samples. *Poa compressa* and *Aristida purpurascens* have consistently high values. *Rumex Acetosella* was also widely encountered, but most of the individuals were small and depauperate. Species of intermediate frequency included *Hedeoma pulegioides*, *Solidago nemoralis*, *Gnaphalium obtusifolium*, and *Erigeron canadensis*. None of the other species found was encountered in more than 30 per cent of the quadrats sampled. These frequency values indicate the predominant influence of the two grasses in the community.

Biomass Determinations

The relative importance of *P. compressa* and *A. purpurascens* is also borne out by biomass determinations made during the summer and fall of 1949 and 1950. Nineteen 0.5-square-meter quadrats were clipped as close to the ground surface as possible. The air-dry weights in grams of the collected material are shown in Table V. *P. compressa* and

TABLE V

Biomass Determinations of Vegetation from Nineteen Clipped Quadrats (0.5 sq.m. each) in *Poa-Aristida* Community, Edwin S. George Reserve, Late Summer and Fall, 1949 and 1950

Species	Air-dry Weights (Grams) of Clipped Material		
	Total Weight	Wt./sq.m.	Per Cent of Total
<i>Poa compressa</i>	647.8	68.2	46.0
<i>Aristida purpurascens</i>	430.4	45.3	30.6
<i>Rumex Acetosella</i>	98.3	10.4	7.0
<i>Solidago nemoralis</i>	95.6	10.1	6.8
Other grasses	38.4	4.0	2.7
<i>Danthonia</i> sp.			
<i>Panicum</i> sp.			
<i>Poa</i> sp.			
<i>Antennaria fallax</i> and <i>A. neglecta</i> ..	22.6	2.4	1.6
Miscellaneous	74.6	7.8	5.3
<i>Ambrosia</i> sp.			
<i>Cyperus</i> sp.			
<i>Erigeron</i> sp.			
<i>Gnaphalium</i> sp.			
<i>Hedeoma</i> sp.			
<i>Hieracium</i> sp.			
<i>Hypericum</i> sp.			
<i>Lactuca</i> sp.			
<i>Lespedeza</i> sp.			
<i>Liatris</i> sp.			
<i>Oxalis</i> sp.			
<i>Polygonum</i> sp.			
<i>Potentilla</i> sp.			
<i>Solidago</i> sp.			
Total	1407.7	148.2	100.0

A. purpurascens greatly outweighed the remaining material and together composed 76.6 per cent of the total dry weight of the clippings. *Rumex Acetosella* and *Solidago nemoralis* were the only other species to exceed 5 per cent of the total weight. All other species taken together comprised less than 10 per cent of the total weight.

Density and Spacing

We have as yet made no effort to estimate the coverage for the various species of the *Poa-Aristida* community. Coverage is difficult to measure with a satisfactory degree of accuracy in mixed grass-forb communities. Information about the density of individual plants or culms was obtained from the clipped quadrats described above. The average numbers of individuals counted on these quadrats are shown in Table VI. *P. compressa*

TABLE VI

Counts of Individual Culms or Plants on Nineteen Clipped Quadrats
(0.5 sq.m. each) in *Poa-Aristida* Community, Edwin S. George Reserve,
Late Summer and Fall, 1949 and 1950

Species	Number of Individual Culms or Plants		
	Total Number	No./sq.m.	Per Cent of Total
<i>Aristida purpurascens</i>	5593	588.7	40.8
<i>Poa compressa</i>	5260	553.7	38.3
<i>Rumex Acetosella</i>	1745	183.7	12.7
Other grasses	484	50.9	3.5
<i>Danthonia</i> sp.			
<i>Panicum</i> sp.			
<i>Poa</i> sp.			
<i>Antennaria fallax</i> and <i>A. neglecta</i>	220	23.2	1.6
<i>Solidago nemoralis</i>	131	13.8	1.0
Miscellaneous	286	30.1	2.1
<i>Ambrosia</i> sp.			
<i>Cyperus</i> sp.			
<i>Erigeron</i> sp.			
<i>Gnaphalium</i> sp.			
<i>Hedeoma</i> sp.			
<i>Hieracium</i> sp.			
<i>Hypericum</i> sp.			
<i>Lactuca</i> sp.			
<i>Lespedeza</i> sp.			
<i>Liatris</i> sp.			
<i>Oxalis</i> sp.			
<i>Polygonum</i> sp.			
<i>Potentilla</i> sp.			
<i>Solidago</i> sp.			
Total	13,719	1444.1	100.0

and *A. purpurascens* each exceeded 500 culms per square meter and together comprised 79.1 per cent of all culms and plants on the quadrats. *Rumex Acetosella* was the only other species to exceed 10 per cent of the total, and all other species taken together composed only 8.2 per cent of the total.

Additional data on density and spacing were obtained from a 50-meter transect taken on June 8, 1949. A steel tape of 1-cm. width, calibrated in centimeters, was stretched through a representative part of the *Poa-Aristida* community. The position of each plant rooted under the tape was recorded to the nearest centimeter. This transect was a 1 by 5000 cm. strip, with an area of 0.5 square meters, equivalent to one of the clipped plots. The number of individual culms or plants encountered in the transect and the average distance between adjacent individuals is shown in Table VII. Again, *P. compressa* and *A. purpurascens* predominate; the former had an average spacing of 18.1 cm. between culms and the latter an average spacing of 19.3 cm. In neither species did the frequency distribution of spacing measurements fit a normal curve; 65.3 per cent of the *Poa* culms and 65.2 per cent of the *Aristida* culms were more closely spaced than the average found on the line. Nevertheless, *Poa* occurred in 96 per cent of the 1-meter subdivisions of the transect, and *Aristida* occurred in 100 per cent.

TABLE VII

Numbers of Individual Culms or Plants and Average Distances Between Adjacent Individuals Encountered Along a 50-meter Transect Through the *Poa-Aristida* Community, Edwin S. George Reserve, June 8, 1949

Species *	Number of Culms or Plants	Average Distance Between Adjacent Individuals (cm.)
<i>Poa compressa</i>	276	18.1
<i>Aristida purpurascens</i>	259	19.3
<i>Rumex Acetosella</i>	125	40.0
<i>Antennaria neglecta</i>	28	178.6
<i>Antennaria fallax</i>	25	200.0
<i>Poa pratensis</i>	16	312.4
<i>Solidago nemoralis</i>	11	454.5
<i>Hedeoma pulegioides</i>	10	500.0
<i>Krigia virginica</i>	5	1000.0
<i>Panicum</i> sp.	4	1250.0
<i>Gnaphalium obtusifolium</i>	3	1666.7
<i>Erigeron canadensis</i>	3	1666.7
<i>Liatris aspera</i>	2	2500.0
<i>Hieracium longipilum</i>	2	2500.0
<i>Panicum oligosanthes</i> var. <i>Scribnerianum</i>	2	2500.0

* Total species sampled = 15. Total area sampled = 0.5 sq. m.

COMMUNITY DYNAMICS

The mosaic character of the *Poa-Aristida* community has already been noted. As Watt (1947) pointed out, the significance of pattern in the plant community will be made clear only by an investigation of the processes and changes influencing the pattern. Although we have not yet attempted to make a detailed study of the dynamics of this old-field community, it seems desirable to accompany this preliminary description with a few brief notes on the evidence of succession.

Succession

The presence of scattered junipers, hawthorns, and cherry seedlings, and the marked ecotone with the adjacent oak-hickory woods (Pl. I, Fig. 2, and Pl. II, Fig. 1) are indicative of a general successional trend towards deciduous forest. The rate of succession, however, is slow in comparison with that observed on abandoned fields elsewhere (Thomson, 1943). Probable factors in the retardation of this succession include the general sterility of the soil and the marked effects of over browsing by the herd of deer maintained on the Reserve.

Microsuccessional Cycles

Within this general framework of slow succession there appear to be more rapid microsuccessional changes which repeat themselves over and over. The cycle of these changes bears much similarity to the "regeneration complex" of Watt (1947). The *Poa-Aristida* community seems to include a characteristic developmental pattern of local phases, marked by pioneer, building, mature, and degenerating stages, with the consolidated grass patches representing the mature stage of cycle.

One conspicuous cycle is apparently initiated by the development of patches of mosses, especially *Ceratodon purpureus* or *Polytrichum piliferum*, which invade bare areas and eventually form considerable colonies. Highly social species, such as *Antennaria fallax* and *A. neglecta*, may also be among the pioneers and form many solid, often circular, microstands up to one or two meters in diameter (Pl. II, Fig. 2). The building stage is characterized by the invasion of these patches by *Rumex Acetosella* and *Poa compressa*, and scattered individual seedlings of other grasses and forbs also appear. As the patch approaches maturity the grasses become the dominant plants. Degeneration sets in with the accumulation of many dead culms and stems, which are rapidly covered by *Cladonia* plants of several species. The end of the degenerative stage is marked by the occurrence of very local erosion planes, produced by the joint action of such forces as precipitation, frost, and wind. Such planes often have the erect cormlike rootstalks of dead *Cyperus filiculmis* standing exposed above the level of the bare soil, which is then a few centimeters lower than its original surface. These bare areas are, in turn, the sites of invasion by mosses, various seedlings of forbs, and eventually by the dominant grasses, thus repeating a more or less consistent sequence of events.

Such cycles give the appearance of self-perpetuating systems, at least from a short-term point of view. They are also frequently initiated by the activities of ants, ground squirrels, and other animals which bring considerable quantities of soil to the surface and destroy the previously existing vegetation. The community will not be thoroughly understood until the various processes involved in this sequence are worked out and until the reciprocal relations of plants, animals, and soil are fully explored.

SUMMARY

An abandoned field on the Edwin S. George Reserve, of the University of Michigan in southeastern Michigan, is being investigated to study the organization and operation of a natural community. Two principal community types are recognized within the field: a dense growth of *Poa pratensis*, which characterizes the hollow depressions or swales, and the vegetation of the upland areas, which is dominated by *Poa compressa* and *Aristida purpurascens*. Studies of frequency, biomass, density, and spacing indicate that the prevailing vegetation of the field is a secondary grassland, with which are associated various species common in this region to such comparatively sterile, exposed habitats. Most of the plants of the *Poa-Aristida* community of the upland areas in the field show some tendency towards clumping, and the mosaic or patchwork character of the vegetation is clearly evident. There is a slow successional trend towards deciduous forest, which formerly covered the field and which now adjoins it along much of its periphery. Within the framework of succession there appear to be more rapid microsuccessional changes, which repeat themselves over and over in the form of a cycle, marked by pioneer, building, mature, and degenerating stages, with the established grasses representing the mature stage.

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PLATE I



FIG. 1. Looking northwest from mid-field. The darker vegetation of a swale is seen in the center. E. S. George Reserve, March 19, 1949. S. A. Cain.



FIG. 2. Looking southwest from northern half of field. Note scattered junipers and hawthorns. E. S. George Reserve, August 3, 1949. F. C. Evans.

PLATE II



FIG. 1. Looking north along eastern margin of field, showing ecotone between field and oak-hickory woods. E. S. George Reserve, July 27, 1949. F. C. Evans.



FIG. 2. Detail of vegetation, showing patch of *antennaria fallax*. E.S. George Reserve, August 3, 1949. F. C. Evans.

